On the nematode genus *Heterodorus* Altherr, 1952 (Dorylaimida: Nordiidae) with descriptions of three new species

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Abstract. The genus *Heterodorus* Altherr, 1952 is analysed and redefined. Of the nominal species, four are synonymized, namely *H. magnificus* Altherr, 1952 and *H. thornei* (Baqri & Jairajpuri, 1974) with *H. arcuatus* (Thorne, 1939), *H. bongersi* (Mushtaq, Baniyamuddin & Ahmad, 2007) with *H. brevidentatus* (Thorne, 1939) and *H. satendri* (Baqri & Jairajpuri, 1974) with *H. constrictus* (Jairajpuri & Loof, 1968). Three species, new to science, are described. *Heterodorus unicus* sp. n. from Papua New Guinea is distinguished by its small body (on average 1.23 mm), continuous lip region, short odontostyle as long as lip region width, far posteriorly located D nucleus, greenish intestine, deep vulva, and by a single ventromedial supplement. *Heterodorus monticola* sp. n. from Peru is characterized by its short body (on average 1.36 mm), continuous lip region, short odontostyle as long as 1.1–1.2 lip region widths, far posteriorly widened pharynx, strongly swollen vagina, and by two or three ventromedial supplements. *Heterodorus alius* sp. n. from Papua New Guinea also belonging to the small species (on average 1.22 mm long) shows some atypical or marginal characters: a longer cylindrus, more anteriorly located D nucleus (54–57 %), more anteriorly posited vulva (39–41 %), longer vagina, longer spicula, and a row of six or seven ventromedial supplements beginning closer to the adanal pair as usual. A key to the identification of *Heterodorus* species is added. Finally, an *Enchodelus* species is transferred to *Papuadorus* Andrássy, 2009 as *P. coomansi* (Nicholas & Stewart, 1985) comb. n.

Keywords. Nematoda, Dorylaimida, *Heterodorus*, new species, key to the species.

In the second part of his classic paper on the In the second part of mis characteristics and de-(1952) erected the genus Heterodorus, and described its type species, Heterodorus magnificus Altherr, 1952. He compared it with Enchodelus Thorne, 1939 and distinguished by the somewhat (apparently) different odontophore and the "peculiar" structure of the female gonad. In 1963, he reported on further specimens from Switzerland, and corrected the original description and measurements of *H.magnificus*. In the meantime, three excellent specialists of that time, M. Luc, J. B. Goodey and G. Thorne, checked the type specimens of *H. magnificus*, and *unisono* stated that they belonged to the genus Enchodelus. Both the structure of the odontostyle/odontophore and that of the genital organ corresponded to the usual types in *Enchodelus* species. Therefore, Altherr synonymized Heterodorus with Enchodelus and transferred the Swiss species to the latter genus as Enchodelus magnificus (Altherr, 1952) Altherr, 1963. Later, Siddiqi (1969) also studied Altherr's specimens, and provided fine drawings of the an-

terior and pharyngeal region (Fig. 4 M–N). In that paper, Siddiqi revised the classification of Dorylaimoidea, and accepted *Heterodorus* as valid genus characterized by the position of the second pair of subventral pharyngeal gland nuclei (PS nuclei) lying "considerably anterior to the base of the oesophagus".

Most of subsequent authors left Siddiqi's opinion out of consideration, and regarded *Heterodorus* as junior synonym of *Enchodelus*. Ahmad and Jairajpuri (1980) revised the genus *Enchodelus* and grouped its species under five subgenera. Subgenus *Heterodorus* was one of them including the only species, *E. (H.) magnificus*. The above authors stressed that *Enchodelus* essentially consists of two main groups of species defined by tail shape, either rounded or conical. For the second group, they proposed the new subgenera *Nepalus* (with long odontostyle) and *Paraenchodelus* (with shorter odontostyle). In their book (1992), Jairajpuri and Ahmad followed this classification.

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Recently, Andrássy (2009) expressed the opinion that the genus of Altherr can still be accepted as valid. It includes those *Enchodelus*-like species that have a conoid tail in both sexes, and ventromedial supplements few in number lying in their series at a distance from the adanal pair. Since the above mentioned two subgenera of Ahmad and Jairajpuri, *Nepalus* and *Paraenchodelus*, showed all the main structures of *Heterodorus*, he synonymized them with Altherr's genus. At the same time, Andrássy transferred 24 conical-tailed species from *Enchodelus* to *Heterodorus*.

The genus *Heterodorus* is characterized and differentiated from *Enchodelus* as follows.

Heterodorus Altherr, 1952

Syn. Enchodelus (Heterodorus Altherr, 1952) Ahmad & Jairajpuri, 1980; Nepalus Ahmad & Jairajpuri, 1980; Paraenchodelus Ahmad & Jairajpuri, 1980.

Diagnosis. Nordiidae, Pungentinae. Body ranging in length from 1.0 to 2.8 mm. Cuticle smooth or finely, exceptionally coarsely transversely annulated. Lips amalgamated or slightly separated, lip region not or moderately separated from adjoining body. Odontostyle thin to very thin with small aperture, 10 to 70 µm, one to four times the labial diameter long; odontophore rodlike, lacking basal flanges. Guiding ring double, but thin. Basal expanded part (cylindrus) shorter than half a pharyngeal length, weakly muscular. Anterior pair of pharyngeal nuclei (AS) often inconspicuous, posterior pair (PS) distinct and lying far anterior to basal end of cylindrus, close to the middle of glandularium. Intestine often filled with green-coloured food rests. Prerectum medium long. Female genital system amphidelphic, with bipartite uterus, transverse vulva and occasionally highly developed vagina. Males known in nearly 60 % of the species. Spicula dorylaimoid. Ventromedial supplements one to nine, well spaced, posterior ones lying well anterior to the adanal pair. Tail in sexes similar, short, conoid, ventrally arcuate, with finely rounded tip.

Relationships. Heterodorus shows a fairly constant morphological pattern. It is very similar to Enchodelus Thorne, 1939, but the simple odontophore (vs. basally flanged), bipartite uterus consisting of a proximal wider and a distal narrower section (vs. tripartite consisting of a proximal wider, an intermediate narrower and a distal spherical section), conoid and ventrally arcuate tail (vs. broadly rounded, not curved) and the low number (1-9 vs. 7-16) and arrangement of supplements (their row lying at a distance from the adanal pair, predominantly well outside the range of spicula vs. their row continuous with the adanal pair, and the posteriormost supplement(s) lying in spicular range) clearly distinguish it from its "sister" genus.

Type species. Heterodorus magnificus Altherr, 1952 = Enchodelus arcuatus Thorne, 1939 = Heterodorus arcuatus (Thorne, 1939) Andrássy, 2009 (see Remarks).

Currently, the following 25 species can be classified under *Heterodorus*.

H. alius sp. n.

H. arcuatus (Thorne, 1939) Andrássy, 2009
Enchodelus arcuatus Thorne, 1939
Enchodelus (Paraenchodelus) arcuatus Thorne, 1939 (Ahmad & Jairajpuri, 1980)
Heterodorus magnificus Altherr, 1952 syn. n.
Enchodelus magnificus (Altherr, 1952) Altherr, 1963
Enchodelus (Heterodorus) magnificus (Altherr, 1952) Altherr, 1963 (Ahmad & Jairajpuri, 1980)

Enchodelus thornei Baqri & Jairajpuri, 1974 syn. n.

Enchodelus (Paraenchodelus) thornei Baqri & Jairajpuri, 1974 (Ahmad & Jairajpuri, 1980) Heterodorus thornei (Baqri & Jairajpuri, 1974) Andrássy, 2009

H. brevidentatus (Thorne, 1939) Andrássy, 2009
 Enchodelus brevidentatus Thorne, 1939
 Enchodelus (Paraenchodelus) brevidentatus
 Thorne, 1939 (Ahmad & Jairajpuri, 1980)
 Enchodelus bongersi Mushtaq, Baniyamuddin & Ahmad, 2007 syn. n.
 Heterodorus bongersi (Mushtaq, Baniyamuddin & Ahmad, 2007) Andrássy, 2009

- H. conicaudatus (Ditlevsen, 1927) Andrássy, 2009
 Dorylaimus conicaudatus Ditlevsen, 1927
 Dorylaimellus conicaudatus (Ditlevsen, 1927)
 Thorne & Swanger, 1936
 Enchodelus conicaudatus (Ditlevsen, 1927)
 Thorne, 1939
 Enchodelus (Paraenchodelus) conicaudatus (Ditlevsen, 1927)
 Thorne, 1939 (Ahmad & Jairajpuri, 1980)
- H. constrictus (Jairajpuri & Loof, 1968) Andrássy,
 2009
 Enchodelus constrictus Jairajpuri & Loof,
 1968
 Enchodelus satendri Baqri & Jairajpuri,
 1974
 - **syn. n.**Enchodelus (Paraenchodelus) satendri Baqri & Jairajpuri, 1974 (Ahmad & Jairajpuri, 1980)
 Heterodorus satendri (Baqri & Jairajpuri, 1974)
 Andrássy, 2009
- H. faeroensis (Ditlevsen, 1928) Andrássy, 2009
 Dorylaimus (Doryllium) faeroensis Ditlevsen, 1928
 Enchodelus faeroensis (Ditlevsen, 1928) Thorne, 1939
 Enchodelus (Paraenchodelus) faeroensis (Ditlevsen, 1928) Thorne, 1939 (Ahmad & Jairajpuri, 1980)
- H. geraldi (Winiszewska-Slipińska, 1987) Andrássy, 2009 Enchodelus geraldi Winiszewska-Slipińska, 1987
- H. irregularis (Altherr, 1972) Andrássy, 2009
 Enchodelus irregularis Altherr, 1972
 Enchodelus (Paraenchodelus) irregularis Altherr, 1972 (Ahmad & Jairajpuri, 1980)
- H. liangi (Ahmad, Wu & Shaheen, 2002) Andrássy, 2009
 Enchodelus liangi Ahmad, Wu & Shaheen, 2002
- H. longidens (Jairajpuri & Loof, 1968) Andrássy, 2009
 Enchodelus longidens Jairajpuri & Loof, 1968
 Enchodelus (Paraenchodelus) longidens Jairajpuri & Loof, 1968 (Ahmad & Jairajpuri, 1980)
- H. lushani (Ahmad, Wu & Shaheen, 2002) Andrássy, 2009

- Enchodelus lushani Ahmad, Wu & Shaheen, 2002
- H. maximus (Baqri & Jairajpuri, 1974) Andrássy,
 2009
 Enchodelus maximus Baqri & Jairajpuri, 1974
 Enchodelus (Nepalus) maximus Baqri & Jairajpuri, 1974 (Jairajpuri & Ahmad, 1992)
- H. meghalayensis (Mushtaq, Baniyamuddin & Ahmad, 2007) Andrássy, 2009
 Enchodelus meghalayensis Mushtaq, Baniyamuddin & Ahmad, 2007
- H. monticola sp. n.
- H. morgensis (Loof, 1989) Andrássy, 2009 Enchodelus morgensis Loof, 1989
- H. nepalensis (Zullini, 1973) Andrássy, 2009
 Enchodelus nepalensis Zullini, 1973
 Enchodelus (Nepalus) nepalensis Zullini, 1973
 (Ahmad & Jairajpuri, 1980)
- H. porosus (Guerrero, Liébanas & Peña-Santiago, 2007) Andrássy, 2009
 Enchodelus porosus Guerrero, Liébanas & Peña-Santiago, 2007
- H. rhaeticus (Altherr, 1952) Andrássy, 2009
 Enchodelus rhaeticus Altherr, 1952
 Enchodelus (Paraenchodelus) rhaeticus Altherr, 1952 (Ahmad & Jairajpuri, 1980)
- H. southeyi (Jairajpuri & Ahmad, 1986) Andrássy, 2009
 Enchodelus (Paraenchodelus) southeyi Jairajpuri & Ahmad, 1986
- H. striatus (Thorne, 1939) Andrássy, 2009
 Enchodelus striatus Thorne, 1939
 Enchodelus (Paraenchodelus) striatus Thorne, 1939 (Ahmad & Jairajpuri, 1980)
- H. transsilvanicus (Ciobanu, Popovici, Guerrero & Peña-Santiago, 2010) comb. n.
 Enchodelus transsilvanicus Ciobanu, Popovici, Guerrero & Peña-Santiago, 2010
- H. tropicus (Mushtaq, Baniyamuddin & Ahmad, 2007) Andrássy, 2009
 Enchodelus tropicus Mushtaq, Baniyamuddin & Ahmad, 2007
- H. unicus sp. n.

- H. veletensis (Guerrero, Liébanas & Peña-Santiago, 2007) Andrássy, 2009
 Enchodelus veletensis Guerrero, Liébanas & Peña-Santiago, 2007
- H. zonatus (Jairajpuri & Loof, 1968) Andrássy,
 2009
 Enchodelus zonatus Jairajpuri & Loof, 1968
 Enchodelus (Paraenchodelus) zonatus Jairajpuri & Loof, 1968 (Ahmad & Jairajpuri, 1980)

REMARKS

Some species should be commented.

Heterodorus magnificus. - When in 1963 corrected the description and measurements of Heterodorus magnificus, Altherr compared his species with Enchodelus arcuatus Thorne, 1939 as described by different authors and found a great similarity between them. Indeed, if these two taxa are compared, there is hardly doubt about it whatever they represent the same species. As may be seen in Table 1, the morphometric characters of the two species are practically identical. In addition, they are very similar in the finely striated cuticle, shape of the lip region, length of the cylindrus, shape of the tail and length of its hyaline part. It can be concluded with good reason that the species of Altherr is the same as that of Thorne. Altherr's magnificus should be considered a junior synonym of Thorne's arcuatus.

Heterodorus thornei. – This species also cannot be differentiated from *H. arcuatus*. Their habitus, shape of the lip region, odontostyle, genital organ and tail are very similar. Ahmad and Jairajpuri (1980) separated them in their key by the dubious structure of the odontophore "with poorly developed basal flanges" in thornei, and "rod-like" in arcuatus. Table 1 shows how similar arcuatus and thornei are in their morphometrics as well.

Heterodorus bongersi. – In its morphometrics, this species completely agrees with Heterodorus brevidentatus as described by Thorne (1939) and redescribed by Guerrero and Peña-Santiago (2007)

(see Tab. 2). Mushtaq, Baniyamuddin and Ahmad (2007) mentioned some very small differences between these species, of which the only real is, maybe, the greater length of the prerectum. This latter as such is, however, not enough for accepting the validity of *H. bongersi*.

Heterodorus satendri. — This species seems to be the same as *H. constrictus*. In their key to conical-tailed species, Ahmad and Jairajpuri (1980) give the minor difference: odontophore "rod-like" in *constrictus*, and "with poorly developed basal flanges" in *satendri*. The descriptions and the morphometric data of the two specific taxa well correspond to each other (Tab. 3).

Heterodorus irregularis. – The systematic position of this species is somewhat uncertain. Altherr (1972) described it from Sweden on the basis of three female specimens. The tail shows a transition from the *Enchodelus* to the *Heterodorus* type, it is 1.0–1.2 anal body widths long, conoidrounded, straight with bluntly rounded tip. Not knowing the male characters, this taxon should be classified with some reservations under the genus *Heterodorus*.

Enchodelus coomansi. – Nicholas and Stewart (1985) described this conoid-tailed species from mangrove forests on the coast of south-eastern Australia. After them, their species would key out to the subgenus Paraenchodelus. However, it differs from every species of this group (now: genus Heterodorus) as well as from all the species of Enchodelus (s. str.) by the large number (26–31) of contiguous medioventral supplements. On the other hand, the Australian species, just in the number and arrangement of the supplements, resembles another enchodelid (nordiid) species, Papuadorus amplus Andrássy, 2009. Papuadorus also has an Enchodelus-like habitus and organization, differs however both from Enchodelus and Heterodorus in having a longitudinal vulva and a great number of contiguous supplements. Although the species of Nicholas and Stewart has a transverse vulva, it fits in other morphological respects, especially in the male characters, well into Papuadorus. E. coomansi should herewith be transferred to the Papuan genus as Papuadorus

	H. magnificus (after Altherr, 1952, and 1963)	H. thornei (after Baqri and Jairajpuri, 1974, and Ahmad and Jairajpuri, 1980)	H. arcuatus (after Thorne, 1939, and Guerrero and Peña- Santiago, 2007)
L (mm)	1.45–1.73	1.28–1.67	1.50–1.99
a	26–32	30–35	25–30
b	4.8–6.0	4.8–5.3	5.2-5.9
c	21–32	23–29	24–25
c'	2.0–2.5	2.0–2.4	2.0-2.2
V (%)	52–55	48–57	50–54
Lip region width (μm)	12–13	11–12	12–14
Odontostyle length (µm)	18–20	17–18	18–22
Odontostyle / lip width	1.4–1.5	1.4	1.5–1.6
Pharynx enlarged at (%)	60	60	58–62
Tail length	60–80	55–65	62–80

Table 1. Comparison of some main morphometric characters of *Heterodorus magnificus* Altherr, 1952, *H. thornei* (Baqri & Jairajpuri, 1974) and *H. arcuatus* (Thorne, 1939)

coomansi (Nicholas & Stewart, 1985) **comb. n.** It can be differentiated from the type species by the longer body (2.4–2.9 *vs.* 2.0 mm), shorter odontostyle (23–32 *vs.* 38–40), transverse vulva (*vs.* longitudinal), higher number of supplements (26–31 *vs.* 20–24), and by the straight and more spicate tail (*vs.* tail ventrally arcuate with rounded tip).

DESCRIPTIONS OF NEW SPECIES

Heterodorus unicus sp. n.

(Figs. 1-2)

Holotype female: L = 1.28 mm; a = 31; b = 5.2; c = 35; c' = 1.3; V = 50 %.

Paratype females (n = 5): L = 1.07-1.30 mm; a = 26-34; b = 5.1-5.6; c = 31-35; c' = 1.2-1.4; V = 50-55 %.

Paratype male: L = 1.09 mm; a = 27; b = 5.1; c = 35; c' = 1.1.

General characters. Small nematodes. Body ventrally curved, C- or G-shaped, 40–47 μm wide at mid-region. Cuticle smooth (under optical microscopy), 1.5–2.0 μm thick. Labial region rounded, practically not separated from adjacent neck, 10–11 μm wide, lips amalgamated with very small papillae. Body at posterior end of pharynx 3.2–3.6 times as wide as labial region. Amphid aperture occupying about half of corresponding body width.

Odontostyle very thin and delicate, $10{\text -}11~\mu\text{m}$ long, as long as labial region width; aperture very small, hardly discernible. Odontophore rod-like without basal swelling, $18{\text -}20~\mu\text{m}$ long. Guiding ring double but thin. Pharynx weakly muscled, $210{\text -}245~\mu\text{m}$ long, gradually expanded at its $62{\text -}66~\%$; cylindrus weak. Distance between posterior end of pharynx and vulva $1.6{\text -}1.9$ times as

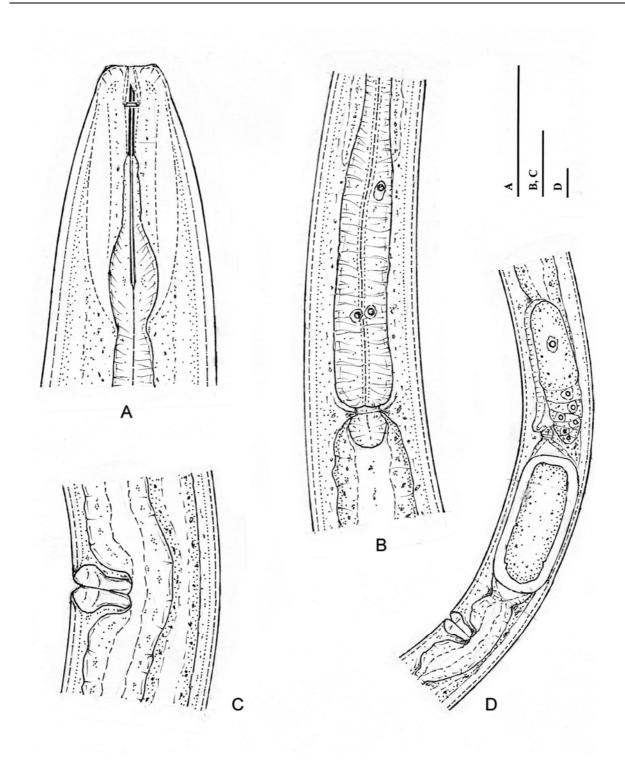


Figure 1. Heterodorus unicus sp. n. A: anterior end; B: posterior pharyngeal region; C: vulval region; D: anterior female gonad. (Scale bars = $20~\mu m$)

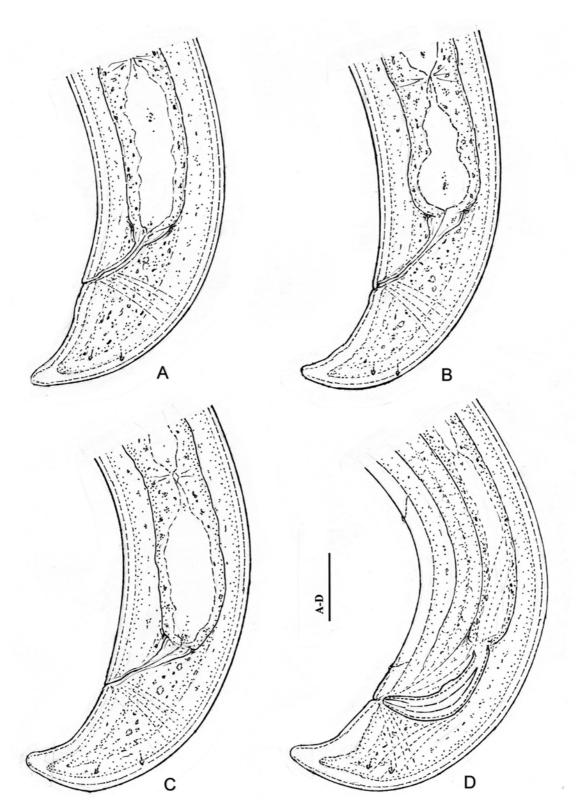


Figure 2. Heterodorus unicus sp. n. A–C: variations of female posterior end; D: male posterior end. (Scale bar = $20 \mu m$)

Table 2. Comparison of some main morphometric characters of *Heterodorus bongersi* (Mushtaq *et al.*, 2007) and *H. brevidentatus* (Thorne, 1939)

	<i>H. bongersi</i> (after Mushtaq <i>et al.</i> , 2007)	H. brevidentatus (after Thorne 1939, and Guer- rero and Peña-Santiago, 2007)
L (mm)	1.33–1.69	1.30–1.86
a	30–38	28–36
b	4.6–5.7	4.8–6.5
С	24–32	24–34
c'	1.7–2.1	1.5–2.4
V (%)	49–54	47–54
Lip region width (μm)	12	11–14
Odontostyle length (µm)	13–14	12–16
Odontostyle / lip width	1.2–1.3	1.1–1.4
Pharynx enlarged at (%)	58–64	54–65
Tail length (μm)	49–65	50–70

Table 3. Comparison of some main morphometric characters of *Heterodorus satendri* (Baqri & Jairajpuri, 1974) and *H. constrictus* (Jairajpuri & Loof, 1968)

	H. satendri (after Baqri and Jairajpuri, 1974, and Ahmad and Jairajpuri, 1980)	H. constrictus (after Jairajpuri and Loof, 1968, and Ahmad and Jairajpuri, 1980)
L (mm)	1.21–1.88	1.28–1.40
a	23–32	21–25
b	4.3–6.3	4.9–5.5
С	23–35	25–36
c'	1.5–1.9	1.5
V (%)	49–58	51
Lip region width (μm)	12–14	10–13
Odontostyle length (µm)	24–29	23–25
Odontostyle / lip width	1.9–2.1	2.0–2.5
Pharynx enlarged at (%)	63–66	60–65
Spicula (µm)	42–52	40–48
Ventromed. supplements	4–6	4–6

long as pharynx. Dorsal pharyngeal nucleus (D) at 73–75 % of pharyngeal length, or 13–14 % of entire length of body. AS nuclei minute, PS nuclei distinct, located at 56–59 % of glandularium. The latter 60–62 μ m long. Cardia conoid-rounded. Intestine either in its total length or in its posterior half filled with green-coloured food (probably moss) rests.

Female. Genital apparatus amphidelphic. Each branch equally developed, 3.8–4.8 body diameters long or occupying 12–15 % of body length. Ovaries reflexed midway to vulva. Vulva a deep transverse slit, vagina 18–22 µm long, extending inwards 38-48 % of corresponding body width. Sphincter between oviduct and uterus present. Each uterus branch consisting of a proximal wider and a distal narrower portion; the former packed with sperms. Three females possess one thickwalled uterine egg each, 95–104×35–38 μm, 2.2– 2.5 times the body width long. Rectum 0.6–1.2, prerectum 1.8-2.5 times as long as anal body width. Vulva-anus distance equal to 13-16 tail lengths. Tail 35-40 µm long or 2.8-3.2 % of total body length, ventrally curved with rather bluntly rounded tip.

Male. Similar in general morphology to female. Testes two, opposed, spermatozoa fusiform, 4–5 μm long. Spicula dorylaimoid, 38 μm long. Adanal pair of supplements at 12 μm from cloaca. Only a single ventromedial supplement present, situated at 60 μm from cloacal opening. Prerectum longer than the former distance. Tail 36 μm long, 2.8 % of entire length of body, ventrally curved, similar to that of female.

Diagnosis and relationships. A small and rather robust member of *Heterodorus*, with body on average 1.23 mm long, continuous lip region, short and delicate odontostyle, well posterior to its middle expanded pharynx, far posteriorly located D nucleus, but anteriorly located PS nuclei, greenish intestine, deep vulva, paired gonads, thick-walled eggs, only one ventromedial supplement, and with short, ventrally curved tail.

In having a small body, narrow lip region, short and very thin odontostyle, *Heterodorus uni*-

cus sp. n. comes closest to H. liangi (Ahmad, Wu& Shaheen, 2002) Andrássy, 2009 described from China and H. meghalayensis (Mushtaq, Baniyamuddin & Ahmad, 2007) Andrássy, 2009 described from India. It differs from H. liangi by the shorter odontostyle (10–11 vs. 13 µm, or 1.0 vs. 1.3–1.4 lip region widths long), normal dorsal pharyngeal nucleus (vs. unusually large), strongly swollen vagina (vs. not or slightly swollen), much shorter prerectum (1.8-2.5 vs. 6-8 anal body widths long), and by the more strongly ventrally curved and narrowly tipped tail (vs. almost stright and more broadly rounded). Unfortunately, the male is unknown in H. liangi. The new species differs from H. meghalayensis by the somewhat shorter odontostyle (10–11 vs. 12–13 µm), shorter tail (1.2–1.4 vs. 2.0–2.1 anal body widths, or 35– 40 vs. 50–53 μm long), more rounded tail tip (vs. sharply tipped), and especially by the presence of a single ventromedial supplement (vs. 4–6 in H. meghalayensis). In the latter respect, Heterodorus unicus sp. n. is unique within the genus. Where males have been described (in 13 other species), they are provided with 2 to 9 ventromedial supplements.

Type specimens. Holotype female on slide No. H-13607. Paratypes: five females, one male and two juveniles. They are deposited in the Department of Systematic Zoology and Ecology of the ELTE University, Budapest.

Type habitat and locality. Mosses from a fallen trunk in a rainforest lowland at Kiunga, a port town on the Fly River in the Western Province of Papua New Guinea; collected in July 1969 by J. Balogh.

Etymology. The species epithet unicus comes from the Latin and means: alone-standing or unique, referring to the single ventral supplement.

Heterodorus monticola sp. n.

(Figs. 3–4)

Holotype female: L = 1.32 mm; a = 38; b = 4.9; c = 38; c' = 1.5; V = 57 %.

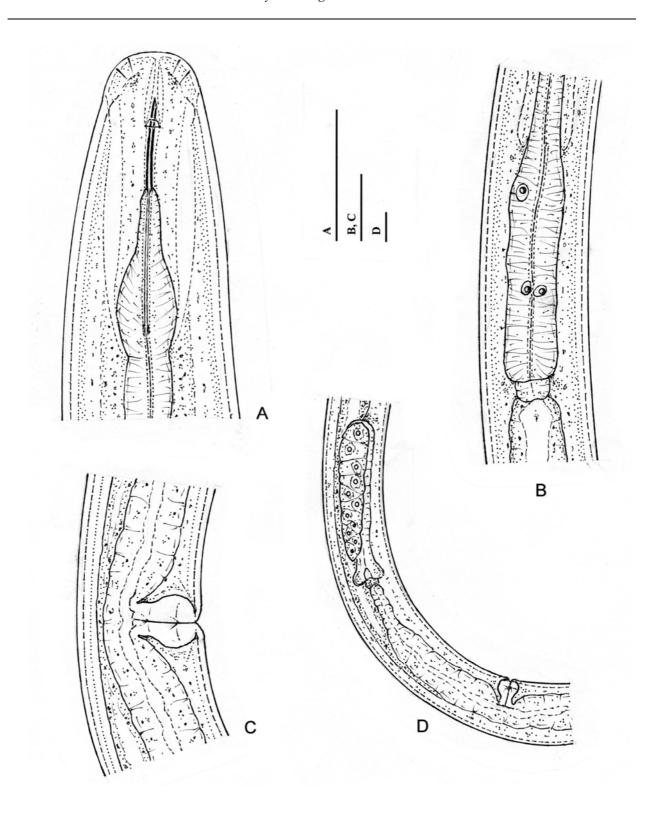


Figure 3. Heterodorus monticola sp. n. A: anterior end; B: posterior pharyngeal region; C: vulval region; D: anterior female gonad. (Scale bars = $20 \mu m$)

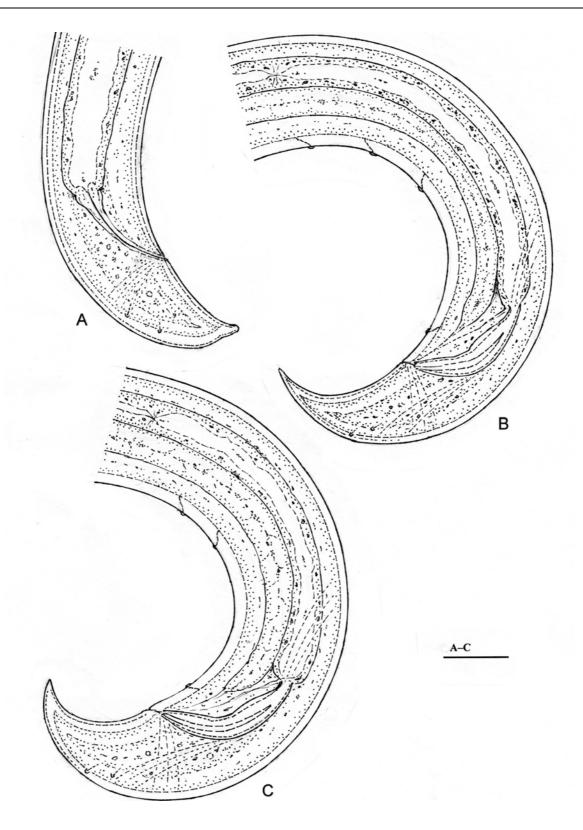


Figure 4. Heterodorus monticola sp. n. A: Female posterior end; B–C: male posterior ends. (Scale bar = $20 \mu m$)

Paratype females (n = 2): L = 1.30-1.45 mm; a = 32-35; b = 5.0-5.4; c = 31-32; c' = 1.5-1.9; V = 54-55 %.

Paratype males (n = 3): L = 1.26–1.46 mm; a = 37–40; b = 4.6–5.6; c = 33–40; c' = 1.2–1.3.

General characters. Body strongly curved, G-shaped after fixation, 34–41 μm wide at mid-region. Cuticle smooth under light microscope, 1.5–2.0 thick on most part of body. Lip region 12–13 μm wide, practically confluent with adjacent neck, lips amalgamated, rounded. Body at posterior end of pharynx 2.6–2.8 times as wide as lip region. Amphids caliciform with aperture occupying half the corresponding body width.

Odontostyle 13–15 μm long, 1.1–1.2 times longer than lip region width, very thin and delicate. Odontophore rod-like, without basal swelling, 21–24 μm long. Guiding ring double but thin. Pharynx weakly muscular, 260–272 μm long, gradually enlarged at 70–74 % of its length. Dorsal nucleus located at 77–82 % of pharyngeal length or 14–17 % of entire length of body. AS nuclei inconspicuous, PS nuclei well discernible, as large as D, located in the middle of glandularium (at 49–54 %). Glandularium 52–56 μm long. Cardia spherical. Intestine transparent, not greenish.

Female. Genital system amphidelphic, each branch 4-6 times as long as mid-body diameter, occupying 12–15 % of body length. Vulva transverse, not sclerotized. Vagina strongly developed, 15 μm broad at its swollen in distal part, 20–22 um long, extending inwards 52-54 % of corresponding body width. Ovaries reflexed about midway to vulva. Each uterine branch consisting of a proximal wider and a distal narrower section. Uterine eggs not observed. Distance between posterior end of pha-rynx and vulva 1.7-1.9 times as long as pharynx. Rectum 1.0–1.2 times, prerectum 2.6-2.8 times the anal body width long. Vulvaanus distance equal to 13-14 tail lengths. Tail 35-48 µm long, 2.6–3.3 % of total body length, conoid, ventrally curved with rounded tip.

Male. In most respects similar to female. Testes two, opposed, spermatozoa fusiform. Spicula dorylaimoid, 44–46 μm, nearly as long as tail.

Adanal pair of supplements located at a distance of $13-14~\mu m$ from cloaca. Ventromedial supplements two in two males and three in one male, situated at 66–68, 84–86 and 102 μm from cloaca, respectively. Prerectum longer than the series of supplements. Tail similar to that of female, 38–42 μm long or occupying 2.5–3.1 % of total length of body.

Diagnosis and relationships. This new species belongs to the smaller representatives of the genus Heterodorus. It is distinguished by its body on average 1.36 mm long, lip region continuous, narrow, odontostyle short, slightly longer than lip region width, pharynx far posteriorly widened, D and PS nuclei large, the former far posterior, the latter in the middle of glandularium, intestine uncoloured, genital system paired, vulva transverse, vagina strongly swollen, two or three ventromedial supplements, and by a short, conical, ventrally curved tail.

In length of the body, the small odontostyle (as long as or only slightly longer than lip region width) and the very posterior location of the D nucleus (at 77-82 % of pharyngeal length), Heterodorus monticola sp. n. resembles H. morgensis (Loof, 1989) Andrássy, 2009. In comparing the present new species with the descriptions of H. morgensis by Loof (1989) from Switzerland, and Guerrero, Liébanas and Peña-Santiago (2007) from the Iberian Peninsula as well as with the paratype specimens (one female and two males) kindly sent by Loof to the present author, it differs by the shorter and plumper tail (35-48 vs. 44-84 μm , c' = 1.5-1.9 vs. 2.0-2.9; tail in *H. morgensis* sharply tipped), the shorter hyaline portion on tail tip, and especially by the lower number of ventromedial supplements (2–3 vs. 4–7).

By having a small body, narrow lip region and short odontostyle, *Heterodorus monticola* sp. n. can also be compared with *H. liangi* (Ahmad, Wu & Shaheen, 2002) Andrássy, 2009, *H. meghalayensis* (Mushtaq, Baniyamuddin & Ahmad, 2007) Andrássy, 2009 and *H. unicus* sp. n. From *Heterodorus liangi* it differs by the broader lip region (12–13 *vs.* 9–10 μm), far posteriorly located D nucleus of normal size (77–82 vs. 64–67 %, and exceptionally large), shorter prerectum

(2.6–2.8 vs. 6–8 anal body widths long, and bythe longer tail (35–48 vs. 26–30 μ m). From *H. meghalayensis* it differs by the more posteriorly located D nucleus (77–82 vs. 71–72 %), tail with rounded tip (vs. sharply tipped), and by the lower number of medioventral supplements (2–3 vs. 4–6). From *Heterodorus unicus* it differs by the somewhat longer odontostyle (13–15 vs. 10–11 μ m), uncoloured intestine, longer spicula (44–46 vs. 38 μ m), and by he number of ventral supplements (2–3 vs. 1).

Type specimens. Holotype female on slide No. H-13661. Paratypes: two females, three males and one juvenile; all deposited in the Department of Systematic Zoology and Ecology of the ELTE University, Budapest.

Type habitat and locality. Soil and detritus from a rainforest (high jungle) at 2600 m above sea level, Oxapampa, Selva Alta Natural Park, eastern side of Pasco Region, Peru; collected in July 1999 by J. Farkas.

Etymology. Latin *monticola* (a noun) means: a mountain inhabitant, referring to the high altitude level where this species was collected.

Heterodorus alius sp. n.

(Figs. 5-6)

Holotype female: L = 1.14 mm; a = 27; b = 5.1; c = 41; c' = 1.2; V = 41 %.

Paratype females (n = 2): L = 1.16-1.25 mm; a = 28-33; b = 5.2-5.3; c = 38-40; c' = 1.3-1.4; V = 39-41 %.

Paratype males (n = 2): L = 1.26-1.30 mm; a = 33-38; b = 5.3-5.5; c = 40-44; c' = 1.1-1.2.

General characters. Body ventrally curved after fixation, more in posterior half, 35–41 μ m wide at mid-region. Cuticle smooth and thin, 1.5 μ m thick on most body. Lip region slightly separated, 11–12 μ m wide, lips amalgamated. Body at pos

terior end of pharynx 3.0–3.5 times as wide as lip region. Amphids caliciform, nearly half as wide as corresponding body.

Odontostyle very thin, 13–14 μm long, only 1.1–1.2 times longer than lip region width. Odontophore simple, 20–24 μm long. Guiding ring thin. Pharynx 210–235 μm long, weakly muscular, enlarged at 52–55 % of its length. Dorsal nucleus less conspicuous, at 54–57 % of pharyngeal length or 10–11 % of total body length. AS nuclei inconspicuous, PS nuclei located at 55–57 % of glandularium. Glandularium 95–103 μm long. Cardia hemispherical. Intestine light green.

Female. Reproductive system amphidelphic, anterior genital branch 3.7-4.6 body diameters long, occupying 13-17 % of body length, posterior branch 4.2-5.0 body diameters long, occupying 15–18 % of body length. Ovaries short, reflexed. Each uterus branch with a proximal wider and a distal narrower part. Uterus-oviduct junction with sphincter. Vulva a transverse deep oval slit, its inner lips not sclerotized. Vagina highly developed, strongly swollen distally, 30-34 μm long, occupying 70–75 % of corresponding body diameter. Uterine eggs not observed. Distance between posterior end of pharynx and vulva only slightly longer (1.1 times) than pharynx. Rectum 1.2-1.4, prerectum 2.5-3.2 anal body widths long. Vulva-anus distance equal to 22-23 tail lengths. Tail 28-31 µm long, occupying 2.4–2.5 % of entire length of body, conoid, slightly bent ventrally with finely rounded tip.

Male. In most respects similar to female. Testes two, spermatozoa fusiform. Spicula 50–52 μm long, much longer than tail. Adanal pair of supplements at 8–10 μm from cloaca. Ventromedial supplements six or seven, the posteriormost levelling with the anterior end of spicula, at 36–38 μm from cloaca, the anteriormost at 150–160 μm from cloacal opening. Tail similar to that of female, slightly ventrally curved, 27–29 μm long, occupying 2.2–2.3 % of entire length of body.

Diagnosis and relationships. Body short, on average 1.22 μm long, lip region slightly offset,

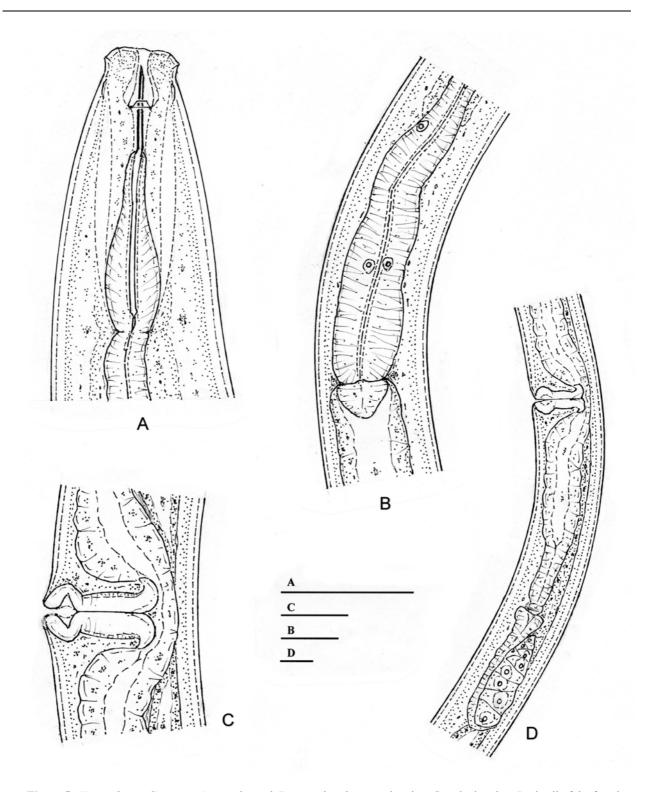


Figure 5. Heterodorus alius sp. n. A: anterior end; B: posterior pharyngeal region; C: vulval region; D: detail of the female gonad. (Scale bars = $20 \ \mu m$)

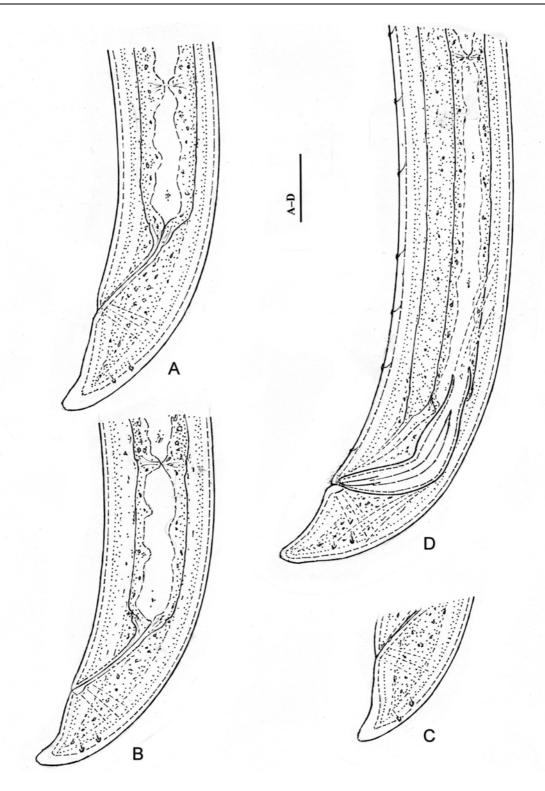


Figure 6. Heterodorus alius sp. n. A–C: female posterior ends; D: male posterior end. (Scale bar = $20 \mu m$)

odontostyle thin and scarcely longer than lip region width, pharynx widened slightly posterior to its middle, D nucleus anteriorly located, PS nuclei in the middle of glandularium, genital system paired, vulva transverse, not sclerotized, anterior to the middle of body, vagina very strongly developed, spicula unusually large, male ventral supplements six or seven, the posteriormost at levelof proximal end of spicula, and tail short, conoid, slightly ventrally curved with finely rounded tip.

Heterodorus alius sp. n. is an interesting taxon within the genus showing a number of marginal values in its morphological characters. Thus, it differs from the general pattern of Heterodorus in having a longer and stronger cylindrus (pharynx enlarged at 52–55 % vs. 56–75 % in other species), a more anteriorly located dorsal pharyngeal nucleus (D = 54–57 vs. 57–82 %), more anteriorly posited vulva (39–41 vs. 41–58 %), very long vagina (70–75 vs. 36–60 % of body diameter), spicula much longer than tail (vs. as long as or shorter than tail, with one exception), and in having the row of ventromedial supplements closer to the adanal pair than usual.

Type specimens. Holotype female on slide No. H-13028. Paratypes: two females, two males and two juveniles. Deposited in the collection of Department of Systematic Zoology and Ecology of the ELTE University, Budapest.

Type habitat and locality. Soil with fallen leaves around Styphelia suaveolens (a kind of shrubs of the family Epacridaceae), 4000 m above sea level, Mt. Wilhelm, highest mountain in Papua New Guinea; collected in September 1968 by J. Balogh.

Etymology. Latin alius means: different or other, referring to the special structures of this new species.

Key to species of Heterodorus

1	Odontostyle 40	μm or	longer (t	o 70	μm)	2
_	Odontostyle 35	μm or	shorter (to 10	μm)	6

2 Body 2.5–2.8 mm long
3 Tail 25 μm, as long as anal body diameter faeroensis (Ditlevsen, 1928)
 Tail 60 μm, nearly twice as long as anal body diameter maximus (Baqri & Jairajpuri, 1974)
4 Odontostyle 65–70 μm long
5 Odontostyle as long as 3–4 labial diameters tail tip sharp
 longidens (Jairajpuri & Loof, 1968) Odontostyle as long as 2–3 labial diameters tail tip rounded geraldi (Winiszewska-Slipińska, 1987)
6 Odontostyle longer, 25–35 μm
7 Tail 25–50 μm long
8 Tail tip sharp; male supplements 4–6
9 Shorter species, 1.1–1.4 mm
10 Tail 70–80 μm long
 11 Lip region 16–18 μm broad; ventral supplements three . zonatus (Jairajpuri & Loof, 1968) – Lip region 12–14 μm broad; ventral supplements six to nine striatus (Thorne, 1939)
12 Tail straight
13 Tail cuticle with numerous "bubbles"
- Tail cuticle simple, without "bubbles"
 14 Two rows of ring-like lateral body pores present porosus (Guerrero et al., 2007) Lateral body pores absent or inconspicuous .15

15	Labial diameter 16–17 μm
_	<i>rhaeticus</i> (Altherr, 1952) Labial diameter 9–14 μm
16 -	Odontostyle 18–22 μm long
	Tail short, 28–32 μm, 1.0–1.1 anal body diameter
18 -	Dorsal pharyngeal nucleus unusually large liangi (Ahmad et al., 2002) Dorsal pharyngeal nucleus normal
19 -	Tail shorter, 1.1–1.4 anal body width long 20 Tail longer, 1.5–2.9 anal body widths long . 22
20 -	Odontostyle 15–16 μm long
	Spicula 50 μm, much longer than tail; supplements 6–7
22	Body 1.6–1.9 mm long
_	Body 1.1–1.5 mm long
23	Tail tip rounded; supplements 2–3
_	Tail tip sharp; supplements 4–7
	Dorsal pharyngeal nucleus at 78–82 %; tail terminus slightly ventrally arcuate
- I	Dorsal pharyngeal nucleus at 71–72 %; tail terminus strongly ventrally bent

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Table 4. Main morphometric characters of Heterodorus species. (In the de Manian ratios, up: females, down: males)

					,				,	,	
	L (mm)	в	q	v	ن .	>	Lip w. (μm)	Odont. (µm/lip w.)	Tail (µm)	Spicula (µm)	Suppl.
alius sp. n.	1.1–1.2	27–33 33–38	5.1–5.3	38-41 40-44	1.2–1.4	39-41	11–12	13–14 (1.1–1.2)	28–31	50-52	2-9
arcuatus (Thorne, 1939)	1.4–2.0	25–35	4.8–6.0	21–32	2.0-2.5	48–57	12–14	18–22 (1.5–1.6)	20–80	42	9
brevidentatus (Thorne, 1939)	1.6–1.9	28–38	4.6–6.5	24–34	1.5–2.4	47–54	11–14	12–16 (1.1–1.4)	49–70	1	1
conicaudatus (Ditlevsen, 1927)	2.0	30	6.1	30	1.4–2.2	42	12	18 (1.4)	36–50	1	1
constrictus (Jairajpuri & Loof, 1968)	1.2–1.9	21–32 23–32	4.3–5.5	23–36	1.5–1.9	49–58	10-14	25–29 (2.0–2.5)	25–50	40–53	4-6
faeroensis (Ditlevsen, 1928)	2.8	26	9	28	1.0	41	91	65 (3.0)	25	1	1
geraldi (Winiszewska-Sl., 1987)	1.7–2.0	27–38	4.5–5.8	30–38	1.5–2.0	49–52	14–16	39–45 (2.7–3.2)	52–58	1	1
irregularis (Altherr, 1972)	1.8–2.0	22–37	7.0–7.3	25–60	1.0–1.2	41–45	10-12	20 . (1.7–2.0)	33–34	1	ı
liangi (Ahmad et al., 2002)	1.1–1.3	28–38	4.1–5.2	43–49	1.2–1.4	46-48	9-10	13 (1.3–1.4)	26–30	1	1
longidens (Jairajpuri & Loof, 1968)	1.5–1.7	24–35 28–37	4.2–5.3 5.2–5.8	30–35 25–34	1.3–1.8	48–51	12–14	40-48 (3.0-4.0)	45–50	95-05	7–8
lushani (Ahmad et al., 2002)	1.3–1.5	27–31	4.6–5.0	47–49	1.0-1.1	45–49	11–12	19–22 (1.5–1.6)	28–32	1	1
maximus (Baqri & Jairajpuri, 1974)	2.5–2.6	41–45	5.8-6.0	41–43	1.8–1.9	49–51	15–18	54–57 (3.5)	60–62	ī	Ĩ
meghalayensis (Mushtaq et al., 2007)	1.0-1.2	26–29 25–30	5.2-5.8	22–24 18–23	2.0–2.1	43–46	11–12	12–13 (1.0–1.2)	50–53	40-46	4-6

Table 4. (continued)

	Г	а	P	၁	د,	>	Lip w.	Odontost.	Tail	Spicula	Suppl.
monticola sp. n.	1.3–1.4	32–38 37–40	4.9–5.4	31–38 33–40	1.5–1.9	54–57	12–13	13–15 (1.1–1.2)	35–48	44-46	2–3
morgensis (Loof, 1989)	1.1–1.5	27–35 30–39	4.4–6.7	18–28 19–31	2.0–2.9	42–52	10-12	(1.0-1.1)	46-84	45–56	4-7
nepalensis (Zullini, 1973)	2.0–2.3	23–36 37	5.0–7.1	30–45 40	1.5–2.4	43–53	16–18	65–70 (4.3)	46–83	09	S
porosus (Guerrero et al., 2007)	1.4–1.7	36–50	7.2	32–36 30–39	1.9–2.5	50–55	11–12	16–18 (1.4–1.6)	40-48	39-45	9-4
rhaeticus (Altherr, 1952)	1.6-2.0	29–35	2-9	29–38	1.6–1.7	40-41	16–17	22 (1.4)	20	1	1
southeyi (Jairajpuri & Ahmad, 1986)	1.1-1.4	23–27 23–27	4.5–5.0	21–23 21–30	1.8–2.0	43-48	10-12	30–33 (2.5–3.2)	49-64	41–42	4
striatus (Thorne, 1939)	1.6–2.0	25–32 27–37	5.1-6.7	28-40 25-32	1.6–1.9	45-49	12–14	35–38 (2.5–3.0)	50–59	51–58	6-9
transsilvanicus (Ciobanu et al., 2010)	1.3–1.5	22–30 27–30	4.6–5.1	28–36 26–30	1.3–1.5	45-48	12–13	29–34 (2.1–2.6)	-42-47	47–50	8-9
tropicus (Mushtaq et al., 2007)	1.0-1.1	26–29	3.5–3.8	30–39	1.1–1.4	44-47	11–12	15–16 (1.3–1.4)	24–34	ſ	ı
unicus sp. n.	1.1–1.3	26–34 27	5.1–5.6	31–35 35	1.2–1.4	95-05	10-11	(1.0)	35-40	38	-
veletensis (Guerrero et al., 2007)	1.8–2.0	34–36	4.9–5.3	23–26	2.3–2.6	48–52	16–18	29–31 (1.6–1.9)	72–78	1	1
zonatus (Jairajpuri & Loof, 1968)	1.6–2.0	35–39 36	4.6–5.8	28–36 33	1.9–2.2	46–50	16–18	34–35 (2.0)	54-62	52	3
From – to (range)	1.0–2.8	21–50	3.5–7.2	18-49	1.0–2.9	40–58	9–18	10–70 (1.0–4.3)	24–84	38–60	1–9

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